

Hybridization and the evolution of invasiveness in plants and other organisms

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Abstract Less than a decade ago, we proposed that hybridization could serve as a stimulus for the evolution of invasiveness in plants (Ellstrand and Schierenbeck *Proc Nat Acad Sci USA* 97:7043–7050, 2000). A substantial amount of research has taken place on that topic since the publication of that paper, stimulating the symposium that makes up this special issue. Here we present an update of this emergent field, based both on the papers in this volume and on the relevant literature. We reevaluate the lists that we presented in our earlier paper of reports in which hybridization has preceded the evolution of invasiveness. We discard a few cases that were found to be in error, published only as abstracts, or based on personal communication. Then we augment the list

from examples in this volume and a supplementary literature search. Despite the omissions, the total number of cases has increased. Many have been strengthened. We add a list of cases in which there has been evidence that *intra*-taxon hybridization has preceded the evolution of invasiveness. We also provide a number of examples from organisms other than plants. We consider how our examples suggest mechanisms whereby hybridization may act to stimulate the evolution of invasiveness. Hybridization does not represent the only evolutionary pathway to invasiveness, but it is one that can explain why the appearance of invasiveness often involves a long lag time and/or multiple introductions of exotics.

Keywords Evolution · Gene flow · Hybridization · Invasive plants · Weeds

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Introduction

In 2000, we proposed that hybridization could serve as a stimulus for the evolution of invasiveness in plants (Ellstrand and Schierenbeck 2000). Lineages with a history of hybridization may enjoy one or more potential genetically-based benefits relative to their progenitors, such as an increase in genetic diversity. In our original paper, we supported our hypothesis with a list of more than two dozen examples of plant lineages known to have become invasive after a history of intertaxon hybridization.

Important to our argument and occupying much of the text of that paper was our assertion that invasiveness could evolve. For example, if hybrid-derived genotypes enjoy increased fitness compared to parental genotypes, that alone could play the causative role in the appearance of invasiveness (Ellstrand and Schierenbeck 2000). Although we were not the first to propose the evolution of invasiveness (e.g., Blossey and Nötzold 1995), the idea was controversial enough to defend. But now, the idea that invasiveness can sometimes result from evolutionary change is no longer controversial (Lee 2002; Lambrinos 2004; Schierenbeck and Ainouche 2005; Suarez and Tsutsui 2008).

Hybridization as an evolutionary stimulus for invasiveness has given life to a new field of study. Our original paper, about 7 years old at the time of this writing, has been cited 332 times (Google Scholar; verified 28 April 2008). The burgeoning interest in the topic catalyzed the creation of a symposium at the 2006 Annual Meeting of the Botanical Society of America. Most of the papers in this volume are derived from that symposium. They present examples of the current state of the field that is moving beyond simple documentation to experimental and descriptive verification and hypothesis testing about how invasiveness evolves in lineages with a hybrid history.

Indeed, in the past few years a considerable amount of research has been conducted on the topic of hybridization as a catalyst for invasive evolution not only in plants, but other organisms as well. Several new plant examples have been found. Also, some of the examples reviewed in our prior paper have been the object of more thorough research that has confirmed their hybrid origin (e.g., Hegde et al. 2006). In a few cases, more thorough study has revealed that the hypothesis of hybrid origin is in error (e.g., Houghton-Thompson et al. 2005; Burger et al. 2006). In addition, there are a growing number of studies finding evidence of *intra*-taxon hybridization preceding the evolution of invasiveness (e.g., Culley and Hardiman 2008).

We define “intertaxon hybridization” here as gene flow, either bi- or unidirectional, between two named taxa, at any taxonomic level and including species, subspecies, variety, or forma. We view “intrataxon hybridization” as gene flow among populations of a single taxon at the species level

or below. Hybridization occurs along a continuum of genetic separation from the population to the species level. Significant differentiation varies with both time and the idiosyncrasies of evolutionary processes subsequent to allopatry, resulting in unrecognized strong population genetic structure in some cases and named taxonomic entities in others. Despite the sometimes unnatural basis of human-created taxonomic definitions (Levin 1979), hybridization and its accompanying evolutionary processes have been accelerated by anthropogenic actions. In the last few centuries, human transport and commerce have moved plants over long distances at unprecedented rates, leading to increasing opportunities for hybridization.

Here we review what is currently known regarding the topic. We reevaluate and augment the examples presented in our 2000 paper. Next, we use our new dataset to give insight into the mechanisms by which invasiveness may evolve. Finally, we examine recently published cases suggesting that hybridization between previously isolated populations of the same species has also lead to the evolution of new invasives.

Materials and methods

We sought well-documented examples of the evolution of invasiveness in plants after a spontaneous hybridization event. Our starting point was our list of examples in our 2000 paper. In order to be consistent, we use the same criteria but we removed cases subsequently found to be in error and then augmented our new list with a literature search.

We used the following criteria for choosing our examples:

- (i) More evidence than intermediate morphology must be available to support the hybrid origin of the invasive lineage. Intermediate morphology does not necessarily support the hypothesis of hybridity (Rieseberg and Ellstrand 1993). Species-specific genetically based traits such as chromosomes, isozymes, and/or DNA-based markers provide more reliable evidence for hybrid parentage. The hypothesis also can receive support from comparison of artificially synthesized hybrids with the putative

spontaneous hybrids or from the relative sterility of the putative hybrids compared with that of the parental species.

- (ii) The hybridization event preceding the evolution of invasiveness must be spontaneous. Many artificial hybrids, especially ornamentals, have escaped from cultivation to become naturalized invasives (e.g., certain mints, comfrey, poplars, and watercress; cf. ref. Stace 1975).
- (iii) The hybrid derivatives must be established as a novel, stabilized lineage and not simply as transient, localized hybrid swarms. In some cases, genetic or reproductive mechanisms may stabilize hybridity (e.g., allopolyploidy, permanent translocation heterozygosity, agamospermy, and clonal spread; cf. ref. Grant 1981). Some hybrid derivatives have become new, reproductively isolated, recombinant species. In other cases, introgression may be so extensive that the hybrid lineage swamps out one or both of its parents, becoming a coalescent complex.
- (iv) The new lineage must exhibit invasiveness. For the purposes of our analysis, we define invasive populations as those that are capable of colonizing and persisting in one or more ecosystems in which they were previously absent. The minimal criterion of invasiveness for our hybrid derivative is that it must replace at least one of its parental taxa or occupy a habitat in which neither parent is present. We hold to this criterion for those few cases in which one parent is itself invasive. We recognize that this definition is highly restrictive, but it sets a clear limit so that we are not tempted to “pad” our list. We recognize that the real definition of invasiveness is much broader, but one that is “fuzzy” for the purpose of our task here.
- (v) We strengthened our list of examples compared to our earlier analysis by excluding those cases published only as abstracts or based solely on personal communication.

We did not restrict ourselves to examples of hybridization involving one or more non-natives, because the evolution of invasiveness by hybridization should be independent of the geographical source of the parental material. Despite the fact that

our literature search is thorough, we caution that our list may be far from exhaustive, especially because the field is now lively, and new studies are arriving at an increasing pace.

Results and discussion

Our 2000 paper included 28 examples in which hybridization preceded invasiveness, four have been eliminated due to lack of support and 11 new examples have been added. In addition, eight examples have been bolstered by new data. In all, we found 35 examples representing 16 plant families in which hybridization preceded invasiveness; these examples are detailed in Tables 1 and 2. Examples of invasive lineages with a putative hybrid origin (e.g., *Lonicera* × *bella* and *Oenothera wolfii* × *Oenothera glazioviana*) were removed because they did not sufficiently meet our criteria, mostly because only morphology has been offered to support their hybridity.

For some of our examples, the hybrid-derived lineage has achieved a taxonomic epithet (Table 1). In other cases, a new invasive lineage has been identified and studied but not yet named, to our knowledge (Table 2). In the associated Tables, we give the parental taxa, plant family, the hybrid derivative’s habit, its site of origin, and the nature of the evidence supporting a history of hybridization for the new lineage. We give one or two good supporting references for each example. In many cases, the best reference is an article or review that cites many supporting sources of empirical research. Finally, we present how the novel lineage is maintained and indicate the scope of its invasiveness.

Despite discarding the weak or disproven cases presented in our earlier article, our new list represents about a 30% increase in examples in less than a decade. The trends that we identified from our original list tend to be reinforced in our new sample. Most of our examples are herbaceous and most are perennial. As noted by Grant (1981) and in our original paper these characteristics are frequently correlated with a tendency for frequent spontaneous hybridization.

In our previous paper (Ellstrand and Schierenbeck 2000) we suggested and discussed four different

Table 1 Invasive taxa that evolved after intertaxon hybridization

Derived taxon	Com-pared to E&S 2000?	Parent taxa	Family	Habit of hybrid lineage	Site of taxon's origin	Data ^a	Ref.	How stabilized?	Invasiveness
<i>Anelanchier erecta</i>		<i>A. humulus</i> × <i>A. "clade B"</i>	Rosaceae	Shrub	N. Amer.	N	Campbell et al. (1997)	Agamospermy	Highly invasive relative to parents
<i>Bromus hordeaceus</i>	More data	<i>B. arvensis</i> × <i>B. scoparius</i>	Poaceae	Ann grass	Europe	C, I, N	Ainouche et al. (1999)	Allopolyploid	Aggressive weed
<i>Cardamine insueta</i>		<i>C. rivularis</i> × <i>C. amara</i>	Brassicaceae	Per herb	Europe	C, N, O	Urbanska et al. (1997)	Allopolyploid	Successfully colonizing disturbed sites
<i>Cardamine flexuosa</i> ("Astar")	New	<i>C. fallax</i> × <i>C. scutata</i>	Brassicaceae	Per herb	Asia	C, O, N	Lihova et al. (2003)	Allopolyploid	Weed in human disturbed sites
<i>Cardamine schultzii</i>		<i>C. rivularis</i> × <i>C. amara</i>	Brassicaceae	Per herb	Europe	C, N, O	Urbanska et al. (1997)	Allopolyploid	Successfully colonizing disturbed sites
<i>Circaea × intermedia</i>		<i>C. alpina</i> × <i>C. lutetiana</i>	Onagraceae	Per herb	Europe	AS, S	Stace (1975)	Clonal growth	Sometimes a weed, often occurs in the absence of one or both parents
<i>Fallopia × bohemica</i>	More data	<i>F. japonica</i> ^a × <i>F. sachalinensis</i> ^a	Polygonaceae	Shrub	Europe	C, N, S	Bailey et al. (2008)	Clonal growth	Noxious weed
<i>Glyceria × pedicellata</i>		<i>G. fluitans</i> × <i>G. notata</i>	Poaceae	Per grass	Europe	S	Stace (1975, 1991)	Clonal growth	"Example of a successful... Sterile hybrid"
<i>Helianthus annuus</i> spp. <i>texasus</i>		<i>H. annuus</i> ^a × <i>H. debilis</i> spp. <i>cucumerifolius</i>	Asteraceae	Ann herb	N. Amer.	C, N, O	Rieseberg et al. (1990)	Recombinant	Weed of disturbed areas
<i>Mentha × verticillata</i>		<i>M. quatica</i> × <i>M. arvensis</i>	Lamiaceae	Per herb	Europe	S	Stace (1991)	Clonal growth	Often in the absence of either parent
<i>Nasturtium sterile</i>		<i>N. microphyllum</i> × <i>N. officinale</i>	Brassicaceae	Per herb	Europe	C	Bleeker et al. (1999)	Recombinant	Weed of disturbed areas
<i>Oenothera glazioviana</i> (<i>O. erythrosepala</i> , <i>O. lamarkiana</i>)		<i>O. hookeri</i> ^a × <i>O. biennis</i> ^a	Onagraceae	Bien herb	Europe	AS, C	Cleland (1972)	Permanent translocation heterozygosity	Weed
<i>Pennisetum sieberianum</i>	New	<i>P. glaucum</i> × <i>P. violaceum</i>	Poaceae	Ann grass	Africa	I	Marchais (1994)	Coalescent complex?	Agricultural weed
<i>Rorippa × armoracioides</i>	New	<i>R. austriaca</i> ^a × <i>R. sylvestris</i>	Brassicaceae	Per herb	Europe	C, N, S	Bleeker (2003)	Clonal growth	"Currently spreading ... forms large populations without its parent species"
<i>Salsola</i> sp.	New	<i>S. tragus</i> × <i>S. kali</i> ssp. <i>austroafricanus</i>	Chenopodiaceae	Ann herb	N. Amer.	C, N	Ayres et al. (2008)	Allopolyploid	Unknown as was not recognized as new species until recently
<i>Senecio squalidus</i>	More data	<i>S. aethensis</i> ^a × <i>S. chrysanthemifolius</i> ^a	Asteraceae	Per herb	Europe	I, O	Abbott and Milne (1995); Abbott et al. (2000, 2008)	Coalescent complex	Rapidly spreading

Table 1 continued

Derived taxon	Com-pared to E&S 2000?	Parent taxa	Family	Habit of hybrid lineage	Site of taxon's origin	Data ^a	Ref.	How stabilized?	Invasiveness
<i>Senecio vulgaris</i> <i>var. hibernicus</i>	More data	<i>S. v. var. vulgaris</i> × <i>S. squallidus</i> ^a	Asteraceae	Ann herb	Europe	AS, C, I	Abbott et al. (2000, 2003)	Recombinant	Rapidly becoming common as it spreads
<i>Sorghum alnum</i>		<i>S. propinquum</i> ^a × <i>S. bicolor</i> ^a	Poaceae	Per grass	S. Amer.	C, N	Paterson et al. (1995)	Allopolyploid	Weed
<i>Solanum</i> × <i>edinense</i> <i>ssp. salamanii</i>	New	<i>S. tuberosum</i> ssp. <i>andigena</i> × <i>S. demissum</i>	Solanaceae	Per herb	N. Amer.	C	Hawkes (1990)	Clonal growth	Agricultural weed
<i>Spartina anglica</i>	More data	<i>S. alterniflora</i> ^a × <i>S. maritima</i>	Poaceae	Per grass	Europe	C, I	Ainouche et al. (2008)	Allopolyploid	Ecosystem-altering invasive
<i>Stachys</i> × <i>ambigua</i>		<i>S. palustris</i> × <i>S. sylvatica</i>	Lamiaceae	Per herb	Europe	C, S	Stace (1975)	Clonal growth	Weed
<i>Tragopogon mirus</i>		<i>T. dubius</i> ^a × <i>T. portifolius</i> ^a	Asteraceae	Bien herb	N. Amer.	C, I, N, O	Novak et al. (1991)	Allopolyploid	Substantial increase in range and numbers
<i>Tragopogon miscellus</i>		<i>T. dubius</i> ^a × <i>T. pratensis</i> ^a	Asteraceae	Bien herb	N. Amer.	C, I, N, O	Novak et al. (1991)	Allopolyploid	Substantial increase in range and numbers
<i>Typha</i> × <i>glaucia</i>	New	<i>T. latifolia</i> × <i>T. angustifolia</i> ^a	Typhaceae	Per herb	N. Amer.	C, I, N, O, S	Kuehn et al. (1999)	Clonal growth	Replacing parents and other wetland species

^a Data in addition to morphological evidence: AS artificial synthesis, C cytological, I isozymes, M genetically-based morphological markers, N nuclear DNA, O organelle DNA, S full or partial sterility

mechanisms that could contribute to the evolution of invasiveness in hybrid-derived lineages:

- (1) Evolutionary novelty
- (2) Increased genetic variation
- (3) Fixed heterosis
- (4) Dumping genetic load

Although these mechanisms are not fully mutually exclusive, how a lineage is stabilized may give a clue to which of these are more likely.

Interestingly, a high frequency (ca. 80%) of the unnamed hybrid-derived invasive lineages listed in Table 2 has stabilized via more-or-less freely recombining coalescent complexes. Option 3, fixed heterosis, cannot be a mechanism for these cases. In contrast, list of novel in Table 1, named hybrid-derived invasive taxa is dominated by cases in which allopolyploidy and/or clonal growth are the modes of hybrid stabilization.

Why the difference between the two groups? One possible explanation is that the parents of the examples in Table 2 may be more closely related hybridizing taxa than those in Table 1. Isolating barriers are weak or non-existent. Those hybrid lineages can intermate with their parents. But, for evolutionarily well-differentiated taxa, isolating barriers are much stronger. Hybrids are often highly sterile. Allopolyploidy and clonality would stabilize lineages that would suffer sterility as F1 hybrids while fixing hybridity and novelty (Grant 1981) and as demonstrated in the case of *Spartina anglica* (Ainouche et al. 2008). In virtually all of our examples in both Tables, and consistent with Anderson's (1948) prediction that hybrids will perform better in disturbed habitat, invasive hybrid lineages are most persistent in human altered environments.

Overcoming self-incompatibility through hybridization has resulted in the establishment of invasive genotypes in three examples presented in this special issue. The genetic material to alleviate allelic incompatibility developed via interspecific hybridization in *Spartina* (Sloop et al. 2008) and through intervarietal hybridization between graft and rootstock in abandoned orchards of *Pyrus* (Culley and Hardiman 2008). *Senecio squalidis*, a diploid, hybrid and self-incompatible species, is the parent to three additional species via hybridization with a native self-compatible species, *S. vulgaris* (Abbott et al. 2008). Conversely, there are likely fewer chances for

hybridization in predominantly selfing taxa. Whether hybridization is a lesser threat in invasive taxa that are predominantly selfing due to their potential for outbreeding depression remains to be tested. Recent theoretical (Taylor and Hastings 2005) and empirical studies (Taylor et al. 2004) have demonstrated the importance of Allee effects (mate shortage, self-incompatibility) in the dynamics of biological invasions.

Table 3 provides examples of intraspecific hybridization that have resulted in invasive genotypes. Novel genotypes can be created via the mating of repeatedly introduced cultivars bred for divergent agronomic or horticultural traits (e.g., *Phalaris arundinacea*, *Pyrus calleryana*). Likewise, invasive lineages have been shown to be simply the result of fortuitous mating among individuals that evolved in geographically separated, genetically differentiated populations (e.g., *Schinus terebinthifolius*).

A growing number of other studies suggest a possible relationship between intraspecific hybridization and invasiveness. Many of these systems are worth further exploration (e.g., *Alliaria petiolata* (Durka et al. 2005), *Avena barbata* (Latta et al. 2007), *Centaurea diffusa* (A. Blair, personal communication), *Cirsium arvense* (Slotta et al. 2006), *Passiflora alata* (Koehler-Santos et al. 2006), and *Phragmites australis* (L. Meyerson, personal communication)).

Evolution of invasiveness can arise from mechanisms other than hybridization. In certain cases, researchers have sought hybridization as a potential cause of invasiveness but no evidence of hybridization was found. For example, California's recently evolved weedy rye had been thought to be an interspecific hybrid between cultivated rye, *Secale cereale*, and a wild perennial, *S. montanum* (Suneson et al. 1969). However, Burger et al. (2006) conducted a genetic analysis of *Secale* individuals at 17 molecular loci, comparing the weedy populations with their putative parents. They found no evidence for an interspecific hybrid origin for weedy California rye. Rather they found evidence for a monophyletic origin from the cultivated species. Likewise, some studies have found no evidence of intraspecific hybridization. Wolfe et al. (2007) experimentally tested whether intraspecific hybridization could account for evolution of invasiveness in North American populations of *Silene latifolia*. They

Table 2 Invasive lineages that evolved after intertaxon hybridization

Parent taxa	Compared to E&S 2000?	Family	Habit of hybrid lineage	Site of lineage origin	Evidence beyond morphology	Representative Ref(s)	How stabilized?	Invasiveness
<i>Beta vulgaris</i> ssp. <i>vulgaris</i> ^a × <i>B. v. ssp. maritima</i>	More data	Chenopodiaceae	Annual herb	Europe	C, I, N, O	Sukopp et al. (2005); Viard et al. (2002)	Coalescent complex	Europe's infamous "weed beet"
<i>Carpobrotus edulis</i> ^a × <i>C. chilensis</i>	More data	Aizoaceae	Perennial herb	N. America	AS, I, O	Gallagher et al. (1997); Schierenbeck et al. (2005)	Clonal growth	Replacing one parent
<i>Myriophyllum heterophyllum</i> ^a × <i>M. pinnatum</i> ^a	New	Haloragaceae	Perennial herb	N. America	N, O	Moody and Les (2002)	Clonal growth	Aquatic weed
<i>Onopordum acanthium</i> ^a × <i>O. illyricum</i>	New	Asteraceae	Perennial herb	Australia	N	O'Hanlon et al. (1999)	Coalescent complex	Weed
<i>Oryza sativa</i> ssp. <i>sativa</i> × <i>O. s. ssp. spontanea</i>	New	Poaceae	Annual grass	Asia	I, M	Chapters in Gressel (2005)	Coalescent complex	One of the world's worst agricultural weeds
<i>Raphanusraphanistrum</i> ^a × <i>R. sativus</i> ^a	More data	Brassicaceae	Annual herb	N. America	AS, C, I, S	Hegde et al. (2006)	Coalescent complex	Weed, replaced both parents
<i>Rhododendron ponticum</i> ^a × <i>R. catawbiense</i> ^a		Ericaceae	Perennial herb	Europe	N, O	Milne and Abbott (2000); Abbott et al. (2003)	Coalescent complex	Noxious invasive
<i>Sarcocornia perennis</i> × <i>S. fruticosa</i>	New	Chenopodiaceae	Woody perennial mat-former	Europe	N	Figuerola et al. (2003)	Clonal growth	Taking over a salt-marsh
<i>Spartina alterniflora</i> ^a × <i>S. foliosa</i>		Poaceae	Perennial grass	N. America	AS, C, M, N, O	Ayres et al. (2004); Sloop et al. (2008)	Clonal growth; coalescent complex	Replacing both parents
<i>Tamarix ramosissima</i> ^a × <i>T. chinensis</i> ^a	New	Tamaricaceae	Tree	N. America	N	Gaskin and Kazmer (2008)	Clonal growth; coalescent complex	Most common <i>Tamarix</i> genotype in U.S.
<i>Viola riviniana</i> × <i>V. reichenbach-lana</i>		Violaceae	Perennial herb	Europe	C, N	Neuffer et al. (1999)	Coalescent complex	Invading polluted forests

AS artificial synthesis, C cytological, I isozymes, M genetically-based morphological markers, N nuclear DNA, O organelle DNA, S full or partial sterility

^a Signifies non-native

Table 3 Invasive lineages that evolved after intrataxon hybridization

Derived invasive lineage	Family	Habit of hybrid lineage	Site of lineage's origin	Evidence beyond morphology	Ref.	How stabilized?	Invasiveness
<i>Phalaris arundinacea</i>	Poaceae	Perennialgrass	North America	I	Lavergne and Molofsky (2007)	Coalescent complex	Forms dense stands
<i>Pyrus calleryana</i>	Rosaceae	Tree	North America	N	Culley and Hardiman (2008)	Coalescent complex that has overcome self-incompatibility	Rapidly spreading
<i>Schinus terebinthifolius</i>	Anacardiaceae	Tree	Florida	N, O	Williams et al. (2005)	Coalescent complex	Forms dense, monospecific stands

AS artificial synthesis, C cytological, I isozymes, M genetically-based morphological markers, N nuclear DNA, O organelle DNA, S full or partial sterility

created interpopulation hybrids and grew them in a common garden with plants from within-population crosses. They found no differences in size, reproductive output or survival. Molecular genetic analysis has sought but not supported intraspecific hybridization in invasive populations of *Clidemia hirta* in Hawaii (DeWalt and Hamrick 2004) and *Ligustrum robustum* in the Mascarene Islands (Milne and Abbott 2004).

Ellstrand and Schierenbeck (2000) cautioned that hybridization may be only one of many possible explanations for invasive ability. In this volume, Whitney et al. (2008) have tested this relationship explicitly by asking whether plant families more prone to hybridization (Ellstrand et al. 1996) contain a correspondingly high number of invasive species. In their extensive analysis of four regional floras and two global databases, they found that plant families prone to hybridization do not contain more invaders than those families not prone to hybridization. The lack of correlation between hybridization and invasiveness in a phylogenetic context emphasizes the idiosyncratic nature of invasive species in their new range.

Human-mediated movement of propagules around the globe has resulted in the hybridization of all kinds of organisms, not just plants, creating a full taxonomic array of newly evolved invasives. Some of the most dramatic non-plant examples of evolution of invasiveness after hybridization among historically allopatric taxa are detailed in Table 4. Clearly, the lessons that can be learned from plants can apply to other pest organisms, including those that cause disease.

Management implications and research needs

There is little doubt that hybridization is an important evolutionary mechanism in plants. The concern regarding hybridization and the subsequent evolution of invasiveness is not whether it can happen, but the speed with which humans accelerate this evolutionary process. Human mediated gene flow between congeners or conspecific populations is a form of biotic homogenization both at the genetic and community level (Olden et al. 2004). However, little is known about how non-native taxa or the spread of their foreign alleles to native taxa may affect local

Table 4 Invasive non-plant lineages that evolved after inter- or intra-taxon hybridization

Derived lineage	Parent taxon or taxa	Division/ Phylum	Evidence beyond morphology	References	How stabilized?	Invasiveness
<i>Anolis sagrei</i>	Intrataxon hybridization	Chordata	N	Kolbe et al. (2004)	Coalescent complex	"Highly invasive"
<i>Apis mellifera</i>	Intrataxon hybridization	Arthropoda	N	Pinto et al. (2005)	Coalescent complex	Infamous Africanized bees
"Invasive variety" of <i>Caulerpa racemosa</i>	Intrataxon hybridization	Chlorophyta	N	Durand et al. (2002); but see Nuber et al. (2007)	Clonal growth	Infamous Mediterranean seaweed
<i>Melanoides tuberculata</i>	Intrataxon hybridization	Mollusca	N, O	Facon et al. (2005)	Parthenogenesis	Pantropical invasive; "hybrid lines have outcompeted their parents in natural habitats"
The F3031 Brazilian purpuric fever clone of <i>Haemophilus influenzae</i> biogroup Aegyptius	<i>Haemophilus influenzae</i> × another genus	Bacteria	N	Smoot et al. (2002)	Mostly clonal	Novel disease organism recently evolved from a relatively benign organism
<i>Phytophthora</i> new sp.	" <i>P. cambivora</i> -like species" × "an unknown taxon similar to <i>P. fragariae</i> "	Oomycota	N	Brasier et al. (1999)	Heteroploidy	"New, aggressive <i>Phytophthora</i> pathogen of alder trees in Europe"

adaptation of a species, community composition, or ecosystem function (Levine et al. 2003), even for the most dramatic invasions (Dukes and Mooney 2004; but see Brusati and Grosholz 2006). The role of gene flow from non-native populations in changing ecosystem relationships has not been examined (Sweeney et al. 2004).

The human-mediated movement of non-native plant genotypes is particularly important at the interface of the urban/natural environment. One of the common sources of introduced species that impact native ecosystems are plants intentionally introduced for ornamental and other horticultural purposes (Anderson et al. 2006). Despite the acknowledgement that many popular horticultural species readily hybridize with their native congeners, until very recently, there has been little regard for their genetic impact to native taxa or the invasive ability of their hybrid offspring. For example, hybridization is occurring between cultivars and their native counterparts within the genera *Quercus*, *Pyrus*, *Acer*, *Malus*, *Platanus*, and *Cornus* (Culley and Hardiman 2008; Coart et al. 2003; Petit 2004). Ecological, genetic, and evolutionary study of such systems will provide baseline information about the generality of problems caused by hybridization between exotics and natives. In particular, the rate at which horticultural genotypes and their hybrid derivatives invade native populations will provide new insights into both the immediate as well as the long term impacts human activities within urban and suburban areas may have on the genetic structure of populations in surrounding wildland areas.

Understanding the importance of fitness effects across spatial scales first requires the identification of genomic differences and an assessment of their geographic dispersion (Cronn and Wendel 2004). Olden and Rooney (2006) emphasize the need for the documentation of taxonomic homogenization by tracking taxa through space and time. The distribution of genetic variation in populations of invasive species, and the relative invasiveness of different genotypes remains elusive with few definitive studies outside of agricultural systems (but see Saltonstall 2003; Gaskin and Schaal 2002; Gaskin and Kazmer 2008; Sloop et al. 2008). Of particular need in understanding the dynamics of adaptation and spread, is an assessment of the molecular population genetics of regulatory loci (Purugganan 2000). Natural

selection on phenotypic variants, which will be considerable in generations after interspecific hybridization, may provide positive feedback on spread rate (Hall et al. 2006). More effective management will be improved through an assessment of the vulnerability of developmental stages and the susceptibility of different genotypes to management regimes.

Important questions remain regarding interactions among the genetic, environmental, and anthropogenic phenomena responsible for the spread of invasive hybrid genotypes. The information gained is of both practical and basic significance. For example, determining the population genetic structure of chloroplast and nuclear alleles for most invasive plant hybrid lineages can be used to estimate the relative contributions to migration by pollen versus that by seed (e.g., Ennos 1994; McCauley 1997). Managers can use such information to determine whether a wave of invasion is due primarily to seed or recurrent hybridization.

Significant advances have been made in modeling the likelihood of hybrid formation, differential rates of spread among hybrid genotypes, and the impact of hybridization on the genetic structure of populations (Hall et al. 2006). Hall and Ayres (2008 not in references) provide a summary of recent advances and needs in the development of predictive models for invasive species. Notably needed is the development of models on which to base management strategies when there is a pair of native and non-native species hybridizing at multiple locations.

Hybrid genotypes originating from native and non-native populations present a major obstacle for managers particularly in the context of biological control, yet no models have been developed for this scenario. For example, despite the presence of two introduced moth species on introduced *Salsola tragus* that were experimentally established as effective biocontrol agents, they are ineffective in controlling the invasive genotypes (Ayres et al. 2008). Similarly, the leaf-feeding chrysomelid beetle provides effective control of some populations of saltcedar, but not others (Gaskin and Kazmer 2008).

The role of soil seedbanks as a source of genetic material that may result in hybridization between previously allopatric populations has not been adequately addressed in plant invasions. Seed dormancy is an adaptive trait and although dormancy periods are well-described for many agricultural weeds

(Baskin and Baskin 1998; Dekker 1997, 1999), virtually nothing is known about the importance of this trait or whether it is important for the introduction of novel genetic diversity in invasive plant species. Seed viability for *Cytisus scoparius* can be as long as 60 years; a 2- or 3-year old plant can produce up to 18,000 seeds/year (Parker and Kareiva 1994). Thus, gene flow from seed banks may be considerable. *Chromolaena odorata* (triffid weed), a shrub native to the neotropics and invasive throughout the Pacific Islands, is quite aggressive and even the occurrence of an occasional seedling 6 years past an eradication effort may provide a mechanism by which to introduce genetic variation not previously found in native populations (Waterhouse and Zeimer 2000).

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References

- Abbott RJ, Milne RI (1995) Origins and evolutionary effects of invasive weeds. In: BCPC symposium proceedings: weeds in a changing world, vol 64, pp 53–64
- Abbott RJ, James JK, Irwin JA, Comes HP (2000) Hybrid origin of the Oxford ragwort, *Senecio squalidus* L. *Watsonia* 23:123–138
- Abbott RJ, James JK, Milne RI, Gillies ACM (2003) Plant introductions, hybridization, and gene flow. *Philos Trans R Soc Lond B* 358:1123–1132
- Abbott RJ, Brennan AC, James JK, Forbes DG, Hegarty MJ, Hiscock SJ (2008) Recent hybrid origin and invasion of the British Isles by aself-incompatible species, Oxford ragwort (*Senecio squalidus* L., Asteraceae). *Biol Invasions* (this issue). doi:10.1007/s10530-008-9382-3
- Ainouche M, Bayer RJ, Gourret JP, Defontaine A, Misset MT (1999) The allotetraploid invasive weed *Bromus hordaceus* L. (Poaceae): genetic diversity, origin and molecular evolution. *Folia Geobot* 34:405–419
- Ainouche M, Fortune PM, Salmon A, Parisod C, Grandbastien M-A, Fukunaga K, Ricou M, Misset M-T (2008) Hybridization, polyploidy and invasion: lessons from *Spartina* (Poaceae). *Biol Invasions* (this issue). doi:10.1007/s10530-008-9383-2
- Anderson E (1948) Hybridization of the habitat. *Evolution* 2:1–9

- Anderson NO, Galatowitsch SM, Gomez N (2006) Selection strategies to reduce invasive potential in introduced plants. *Euphytica* 148:203–216
- Ayres DR, Smith DL, Zaremba K, Klohner S, Strong DR (2004) Spread of exotic cordgrasses and hybrids (*Spartina* sp.) in the tidal marshes of San Francisco Bay. *Biol Invasions* 6:221–231
- Ayres DR, Ryan FJ, Grotkopp E, Bailey J, Gaskin J (2008) Tumbleweed (*Salsola*, section *Kali*) species and speciation in California. *Biol Invasions* (this issue). doi:[10.1007/s10530-008-9380-5](https://doi.org/10.1007/s10530-008-9380-5)
- Bailey JP, Bímová K, Mandák B (2008) Asexual spread versus sexual reproduction and evolution in Japanese Knotweed *s.l.* sets the stage for the “Battle of the Clones”. *Biol Invasions* (this issue). doi:[10.1007/s10530-008-9381-4](https://doi.org/10.1007/s10530-008-9381-4)
- Baskin CC, Baskin JM (1998) Seeds: ecology, biogeography and evolution of dormancy and germination. Academic Press, San Diego
- Bleeker W (2003) Hybridization and *Rorippa austriaca* (Brassicaceae) invasion in Germany. *Mol Ecol* 12: 1831–1841
- Bleeker W, Huthman M, Hurka H (1999) Evolution of hybrid taxa in *Nasturtium* R. Br. (Brassicaceae). *Folia Geobot Phytotaxon* 34:421–433
- Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *J Ecol* 83:887–889
- Brasier CM, Cooke DEL, Duncan JM (1999) Origin of a new *Phytophthora* pathogen through interspecific hybridization. *Proc Natl Acad Sci USA* 96:5878–5883
- Brusati ED, Grosholz ED (2006) Native and introduced ecosystem engineers produce contrasting effects on estuarine infaunal communities. *Biol Invasions* 8:683–695
- Burger JC, Lee S, Ellstrand NC (2006) Origin and genetic structure of feral rye in the western United States. *Mol Ecol* 15:2527–2539
- Campbell CS, Wojciechowski MF, Baldwin BG, Alice LA, Donoghue MJ (1997) Persistent nuclear ribosomal DNA sequence polymorphism in the *Amelanchier* agamic complex (Rosaceae). *Mol Biol Evol* 14:81–90
- Cleland RE (1972) *Oenothera*. Cytogenetics and evolution. Academic Press, London
- Coart E, Vekemans X, Smulders MJM et al (2003) Genetic variation in the endangered wild apple (*Malus sylvestris* (L.) Mill.) in Belgium as revealed by amplified fragment length polymorphism and microsatellite markers. *Mol Ecol* 12:845–857
- Cronn R, Wendel JF (2004) Cryptic trysts, genomic mergers, and plant speciation. *New Phytol* 161:133–142
- Culley T, Hardiman N (2008) The role of intraspecific hybridization in the evolution of invasiveness: a case study of the ornamental pear tree *Pyrus calleryana*. *Biol Invasions* (this issue). doi:[10.1007/s10530-008-9386-z](https://doi.org/10.1007/s10530-008-9386-z)
- Dekker J (1997) Weed diversity and weed management. *Weed Sci* 45:357–363
- Dekker J (1999) Soil weed seed banks and weed management. *J Crop Prod* 2:139–166
- deWalt SJ, Hamrick JL (2004) Genetic variation of introduced Hawaiian and native Costa Rican populations of an invasive tropical shrub, *Clidemia hirta* (Melastomataceae). *Am J Bot* 91:1155–1163
- Dukes JS, Mooney HA (2004) Disruption of ecosystem process in western North America by invasive species. *Rev Chil Hist Nat* 77:411–437
- Durand C, Manuel M, Boudouresque CF, Meinesz A, Verlaque M, Le Parco Y (2002) Molecular data suggest a hybrid origin for the invasive *Caulerpa racemosa* (Caulerpaceae, Chlorophyta) in the Mediterranean Sea. *J Evol Biol* 15:122–133
- Durka W, Bossdorf O, Prati D, Auge H (2005) Molecular evidence for multiple introductions of garlic mustard (*Alliaria petiolata*, Brassicaceae) to North America. *Mol Ecol* 14:1697–1706
- Ellstrand NC, Schierenbeck K (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc Nat Acad Sci USA* 97:7043–7050
- Ellstrand NC, Whitkus R, Rieseberg LH (1996) Distribution of spontaneous plant hybrids. *Proc Nat Acad Sci* 93: 5090–5093
- Ennos RA (1994) Estimating the relative rates of pollen and seed migration. *Heredity* 72:250–259
- Facon B, Jarne P, Pointier JP, David P (2005) Hybridization and invasiveness in the freshwater snail *Melanoides tuberculata*: hybrid vigour is more important than increase in genetic variance. *J Evol Biol* 18:524–535
- Figueroa ME, Castillo JM, Redondo S, Luque T, Castellanos EM, Nieva FJ, Luque CJ, Rubio-Casal AE, Davy AJ (2003) Facilitated invasion by hybridization of *Sarcocornia* species in a salt-marsh succession. *J Ecol* 91:616–626
- Gallagher KG, Schierenbeck KA, D’Antonio CM (1997) Hybridization and introgression in *Carpobrotus* spp. (Aizoaceae) in California. II. Allozyme evidence. *Am J Bot* 84:905–911
- Gaskin JF, Kazmer DJ (2008) Introgression between saltcedars (*Tamarix chinensis* and *T. ramosissima*) in the USA invasion. *Biol Invasions* (this issue). doi:[10.1007/s10530-008-9384-1](https://doi.org/10.1007/s10530-008-9384-1)
- Gaskin JG, Schaal BA (2002) Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. *Proc Nat Acad Sci USA* 99:11256–11259
- Grant V (1981) Plant speciation. Columbia University Press, New York
- Gray AJ, Marshall DF, Raybould AF (1991) A century of evolution in *Spartina anglica*. *Adv Ecol Res* 21:1–62
- Gressel J (2005) Crop fertility and volunteerism. CRC Press, Boca Raton
- Hall RJ, Hastings A, Ayres DR (2006) Explaining the explosion: modelling hybrid invasions. *Proc R Soc Lond B* 273:1385–1389
- Hawkes JG (1990) The potato: evolution, biodiversity and genetic resources. Bellhaven Press, London
- Hegde SG, Nason JD, Clegg J, Ellstrand NC (2006) The evolution of California’s wild radish has resulted in the extinction of its progenitors. *Evolution* 60:1187–1197
- Houghton-Thompson J, Prince HH, Smith JJ, Hancock JH (2005) Evidence of hybridization between *Lythrum salicaria* (purple loosestrife) and *L. alatum* (winged loosestrife) in North America. *Ann Bot* 96:877–885
- Koehler-Santos P, Lorenz-Lemke AP, Salzano FM, Freitas LB (2006) Ecological-evolutionary relationships in *Passiflora alata* from Rio Grande do Sul, Brazil. *Braz J Biol* 66: 809–816

- Kolbe JJ, Glor RE, Rodríguez Schettino L, Chamizo Lara A, Losos JB (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431:177–181
- Kuehn MM, Minor JE, White BN (1999) An examination of hybridization between the cattail species *Typha latifolia* and *Typha angustifolia* using random amplified polymorphic DNA and chloroplast DNA markers. *Mol Ecol* 8:1981–1990
- Lambrinos JG (2004) How interactions between ecology and evolution influence cotemporary invasion dynamics. *Ecology* 85:2061–2070
- Latta RG, Gardner KM, Johansen-Morris AD (2007) Hybridization, recombination, and the genetic basis of fitness variation across environments in *Avena barbata*. *Genetica* 12:16–67
- Lavergne S, Molofsky J (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc Natl Acad Sci USA* 104:3883–3888
- Lee CE (2002) Evolutionary genetics of invasive species. *Trends Ecol Evol* 17:386–391
- Levin DA (1979) The nature of plant species. *Science* 204:381–384
- Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc R Soc Lond Ser B* 270:775–781
- Lihova J, Tribsch A, Marhold K (2003) The *Cardamine pratensis* (Brassicaceae) group in the Iberian Peninsula: taxonomy, polyploidy and distribution. *Taxon* 52:783–801
- Marchais L (1994) Wild pearl millet population (*Pennisetum glaucum*, Poaceae) integrity in agricultural Sahelian areas. An example from Keita (Niger). *Plant Syst Evol* 189:233–245
- McCauley DE (1997) The relative contributions of seed and pollen movement to the local genetic structure of *Silene alba*. *J Hered* 88:257–263
- Milne RI, Abbott RJ (2000) Origin and evolution of invasive naturalised material of *Rhododendron ponticum* L. in the British Isles. *Mol Ecol* 9:541–556
- Milne RI, Abbott RJ (2004) Geographic origin and taxonomic status of the invasive privet, *Ligustrum robustum* in the Mascarene Islands. *Heredity* 92:78–87
- Moody ML, Les DH (2002) Evidence of hybridity in invasive watermilfoil (*Myriophyllum*) populations. *Proc Nat Acad Sci USA* 23:14867–14871
- Neuffer B, Auge H, Mesch H, Amarell U, Brandl R (1999) Spread of violets in polluted pine forests: morphological and molecular evidence for the ecological importance of interspecific hybridization. *Mol Ecol* 8:365–377
- Novak SJ, Soltis DE, Soltis PS (1991) Ownbey's *Tragopogons*: 40 years later. *Am J Bot* 78:1586–1600
- Nuber N, Gornik O, Lauc G, Bauer N, Žuljević A, Papeš D, Zoldoš V (2007) Genetic evidence for the identity of *Caulerpa racemosa* (Forsskål) J. Agardh (Caulerpaceae, Chlorophyta) in the Adriatic Sea. *Eur J Phycol* 42:113–120
- O'Hanlon PC, Peakall R, Briese DT (1999) Amplified fragment length polymorphism (AFLP) reveals introgression in weedy *Onopordum* thistles: hybridization and invasion. *Mol Ecol* 8:1239–1246
- Olden JD, Rooney TP (2006) On defining and quantifying biotic homogenization. *Global Eco Biogeogr* 15:113–120
- Olden J, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol Evol* 19:18–24
- Parker IM, Kareiva P (1994) Assessing the risk of invasion in genetically modified crops: an ecological perspective. In: Jones DD (ed) *The biosafety results of field tests of genetically modified plants and microorganisms*. University of California Division of Agriculture and Natural Resources, Oakland, pp 467–470
- Paterson AH, Schertz KF, Lin YR, Liu SC, Chang YL (1995) The weediness of wild plants: molecular analysis of genes influencing dispersal and persistence of johnsongrass, *Sorghum halepense* (L.) Pers. *Proc Natl Acad Sci USA* 92:6127–6131
- Petit RJ (2004) Biological invasions at the gene level. *Div Distrib* 10:159–165
- Pinto MA, Rubink WL, Patton JC, Coulson RN, Johnston JS (2005) Africanization in the United States: replacement of feral European honeybees (*Apis mellifera* L.) by an African hybrid swarm. *Genetics* 170:1653–1665
- Purugganan MD (2000) The molecular population genetics of regulatory genes. *Mol Ecol* 9:1451–1461
- Rieseberg LH, Ellstrand NC (1993) What can molecular and morphological markers tell us about plant hybridization? *Crit Rev Pl Sci* 12:213–241
- Rieseberg LH, Carter R, Zona S (1990) Molecular tests of the hypothesized hybrid origin of two diploid *Helianthus* species. *Evolution* 44:1498–1511
- Saltonstall K (2003) Microsatellite variation within and among North American lineages of *Phragmites australis*. *Mol Ecol* 12:1689–1702
- Schierenbeck KA, Aïnouche ML (2005) Evolutionary consequences of plant invasions. In: Cadotte MW, McMahon SM, Fukami T (eds) *Conceptual ecology and invasions biology: reciprocal approaches to nature*. Kluwer Press, The Netherlands, pp 193–221
- Schierenbeck KA, Symonds VV, Gallagher KG, Bell J (2005) Genetic variation and phylogeographic analyses of two species of *Carpobrotus* and their hybrids in California. *Mol Ecol* 14:539–547
- Sloop CM, Ayres DR, Strong DR (2008) The rapid evolution of self-fertility in *Spartina* hybrids (*Spartina alterniflora* x *foliosa*) invading San Francisco Bay, CA. *Biol Invasions* (this issue). doi:10.1007/s10530-008-9385-0
- Slotta TAB, Rothhouse J, Horvath DP, Foley ME (2006) Genetic diversity of *Cirsium arvense* (Canada thistle) in North Dakota. *Weed Sci* 54:1080–1085
- Smoot LM, Franke DD, McGillivray G, Actis LA (2002) Genomic analysis of the F3031 Brazilian purpuric fever clone of *Haemophilus influenzae* biogroup Aegyptius by PCR-based subtractive hybridization. *Infect Immun* 70:2694–2699
- Stace CA (1975) *Hybridization and the flora of the British Isles*. Academic Press, London
- Stace CA (1991) *New flora of the British Isles*. Cambridge University Press, Cambridge
- Suarez AD, Tsutsui N (2008) The evolutionary consequences of biological invasions. *Mol Ecol* 17:351–360

- Sukopp U, Pohl M, Driessen S, Bartsch D (2005) Feral beets—with help from the maritime wild? In: Gressel J (ed) Crop ferality and volunteerism. Taylor & Francis, Boca Raton, pp 45–57
- Suneson CA, Rachie KO, Khush GS (1969) A dynamic population of weedy rye. *Crop Sci* 9:121–124
- Sweeney BW, Bott TL, Jackson JK, Kaplan LA, Newbold JD, Standley LJ, Hession WC, Horwitz RJ (2004) Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proc Nat Acad Sci USA* 101: 14132–14137
- Taylor CM, Hastings A (2005) Allee effects in biological invasions. *Ecol Lett* 8:895–908
- Taylor CM, Davis HG, Civile JC, Grevstad FS, Hastings A (2004) Consequences of an allee effect in the invasive of a Pacific estuary by *Spartina alterniflora*. *Ecology* 85: 3254–3266
- Urbanska KM, Hruka H, Landolt E, Neuffer B, Mummenhoff K (1997) Hybridization and evolution in *Cardamine* (Brassicaceae) at Urnerboden, Central Switzerland: Bio-systematic and molecular evidence. *Plant Syst Evol* 204:233–256
- Viard F, Bernard J, Desplanque B (2002) Crop-weed interaction in the *Beta vulgaris* complex at the local scale: allelic diversity and gene flow within sugar beet fields. *Theor Appl Genet* 104:688–697
- Waterhouse B, Zeimer O (2002) On the brink: status of chromolaena odorata in Northern Australia. In: Zachariades C, Muniappan R, Strathie LW (eds) Proceedings of the fifth international workshop on biological control and management of chromolaena odorata. Durban, South Africa, pp 66–70, 23–25 October 2000 ARC-PPRI
- Whitney KD, Ahern JR, Campbell LG (2008). Hybridization-prone plant families do not generate more invasive species. *Biol Invasions* (this issue). doi:[10.1007/s10530-008-9390-3](https://doi.org/10.1007/s10530-008-9390-3)
- Williams DA, Overholt WA, Cuda JP, Hughes CR (2005) Chloroplast and microsatellite DNA diversities reveal the introduction history of Brazilian peppertree (*Schinus terebinthifolius*) in Florida. *Mol Ecol* 14:3643–3656
- Wolfe LM, Blair AM, Penna BM (2007) Does intraspecific hybridization contribute to the evolution of invasiveness? An experimental test. *Biol Invasions* 9:1387–3547